

Migration and Genetic Structure of *Salmo salar* and *Salmo trutta* in Northern Swedish Rivers

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Abstract

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This thesis focuses on the migration of Atlantic salmon (*Salmo salar* L.) and sea trout (*Salmo trutta* L.) before, during and after spawning in two northern Swedish rivers and influence of habitats and environmental factors on these activities. In addition, genetic structure of brown trout and genetic impact of stocked salmon and sea trout juveniles from foreign populations on native stocks was studied. Migrations and genetics are related to anthropogenic factors as historical log-floating and hydropower production.

On their spawning migration, radio-tagged salmon (n=128) and sea trout (n=86) showed that salmon mainly migrated directly to their spawning area, while sea trout exhibited several up- and downstream migrations. Migration speeds was lowered or delayed at steep sections and was higher (25 km d⁻¹) later in the migration period compared to early in the run (8 km d⁻¹) and negatively correlated with water flow. Salmon and sea trout spawned in the main stem in the river Vindelälven, 230 km and 60 km upstream, respectively, while sea trout in the river Piteälven spawned in various tributaries. A majority (90%) of the sea trout survived after spawning and overwintered in the rivers. These kelts migrated seaward in spring at water temperatures of 4–6°C whereafter 69% and 25% was lost at power-station passage in the rivers Vindelälven and Piteälven, respectively.

Genetic differentiation among brown trout with different life histories was high ($F_{ST}=0.09$) while weak differentiation among sea migrating populations was revealed (maximum F_{ST} of 0.03). There was no correlation between genetic and geographic distance among all samples while among samples within the Vindelälven such relationship was significant. Within the Piteälven a subpopulation of sea trout was found in one tributary. Genetic assignment supported that tagged sea trout was homing to this stream. Despite longterm stocking of foreign salmon stocks in the river Sävarån mixed-stock analysis were unable to detect genetic introgression. Likewise, genetic impact of stocking sea trout in the Sävarån seemed low, however, with overlap in genotypes genetic introgression could not be ruled out.

Restorations of connectivity and river habitats were hypothesized to positively influence salmon and sea trout production and gene flow among populations.

Keywords: spawning migration, genetic structure, homing, genetic assignment, power-station, radio tag, stocking, kelt.

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Papers I-VI

This thesis is based on the following papers, which will be refereed to by their Roman numerals:

- I. Nilsson, C., Lepori, F., Malmqvist, B., Törnlund, E., Hjerdt, N., Helfield, J.M., Palm, D., Östergren, J., Jansson, R., Brännäs E. & Lundqvist, H. 2005. Forecasting environmental responses to restoration of rivers used as log floatways: an interdisciplinary challenge. *Ecosystems*. 8, 779-800.
- II. Lundqvist, H., Östergren, J. & McKinnell, S.M. 2006. Interannual variation in distance of spawning migration of radio tagged wild Atlantic salmon (*Salmo salar* L.) females. Manuscript.
- III. Östergren, J., Lundqvist, H. & Nilsson, J. 2006. Individual variation in spawning migration and spawning site selection of sea trout (*Salmo trutta* L.) in two northern Swedish rivers. Manuscript.
- IV. Östergren, J. & Nilsson, J. 2006. Population genetic structure of brown trout (*Salmo trutta* L.) with different life histories in two northern Swedish rivers. Manuscript.
- V. Östergren, J. & Rivinoja, P. 2006. Overwintering and downstream migration of sea trout (*Salmo trutta* L.) kelts in two flow regulated rivers in northern Sweden. Submitted manuscript.
- VI. Nilsson, J., Östergren, J., Lundqvist, H. & Carlsson, U. 2006. Do stockings of non-native salmon and sea trout juveniles affect the genetic stock identity of the wild populations? Manuscript.

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Introduction

The brown trout (*Salmo trutta* L.) and the Atlantic salmon (*Salmo salar* L.) are two iconic fish species in rivers and streams in northern Sweden due to their historical, economical and social value. These species invaded northern Europe when the ice melted about 10 000 years ago (Nilsson *et al.*, 2001; Säisä *et al.*, 2005). The colonization history of brown trout is less well-studied but Garcia-Marin *et al.* (1999) suggested that brown trout in the Baltic Sea belonged to an Atlantic lineage. The anadromous form of brown trout is commonly named sea trout. Elliot (1994), Bagliniere & Maisse (1999), Jonsson (1985; 1989) and Jonsson & Jonsson (2006) have shown that the brown trout is one of the most plastic species among fishes with life-history strategies of remaining in a stream or a lake for their whole life, or undertaking feeding migrations from a stream to a lake or the sea. Ferguson (1989) concluded that the brown trout is one of the most genetically variable vertebrate species. The life histories of sea trout and salmon are relatively similar but they are ecologically separated through differences in spawning time and habitat preference (Degerman *et al.*, 2001, Klementsén *et al.*, 2003; Jonsson & Jonsson, 2006). Both species reproduce in running waters so regardless of migratory habits, they need open migration routes in watersheds to reach suitable spawning habitats.

During the last couple of hundred years, humans have used running waters for a number of purposes. In the 1530s, the Swedish king, Gustav Vasa, claimed ownership of the large northern Swedish salmon rivers for the state (Hvarfner, 1964) which thereafter controlled the in-river fisheries for salmon and sea trout. Byström (1868) reported an historically high catch of 511 salmon in one day in 1824 in the lower part of the river Umeälven. Likewise, he found relatively low abundances of salmon in the catches during the middle of the 19th century. Byström (1868) summarized his observations of the effect of timber floating, damming of lakes, and the fisheries. He concluded that these activities had a negative effect on salmon reproduction and that there was need to restrict salmon fisheries to ensure sustainability. In Sweden, log floating occurred during 1850–1970, with a peak just before World War II. Log floating contributed to the industrialization of Sweden during the 19th century and the first part of the 20th century (Schön, 2000). In northern Sweden, sawmills and pulp mills were situated along the coast (Östlund *et al.*, 1997). Logs were transported from inland using the large northern rivers and their tributaries. To facilitate log transport and prevent logjams, obstructions were removed using dynamite and black powder to blow away large boulders and rocks. Box booms and guiding booms were constructed in rivers, such that side arms often were cut off and bays and productive shallow waters were eliminated (Törnlund, 2002). In addition, large in-river systems of splash dams were created throughout many watersheds (Törnlund, 2002).

The historical log floating together with hydro-electric production are the two main factors that have had the highest and worst impact on the geomorphology of rivers and creeks in this area (Nilsson *et al.*, 2005). Thus, many rearing and spawning habitats that are important for anadromous salmonids have been damaged. McKinnell (1998) and Rivinoja (2005) described how these major impacts, together with the mixed-stock sea fishery in the Baltic Sea, have negatively affected the long-term viability of natural salmonid stocks in northern Baltic rivers. Today, many wild stocks have been lost and only 12 of 44 rivers still

support natural production of salmon in the Gulf of Bothnia (McKinnell, 1997; ICES, 2006). To mitigate for the loss of natural spawning, hatcheries were constructed and large compensatory stocking programs were initiated (Lindroth, 1963; 1965). At present c. 2 million hatchery reared salmon and 350 thousand sea trout juveniles are released into the Baltic Sea every year from Swedish hatcheries located in the lower parts of flow regulated rivers (Laikre *et al.*, 2006). All Baltic countries have similar release programs of salmon and sea trout (ICES, 2006).

Research on wild salmonids in the Baltic Sea has focused on salmon population and evolutionary genetics (Ryman & Ståhl, 1981; Nilsson *et al.*, 2001, Vasemägi, 2004; Säisä *et al.*, 2005), fisheries management implications (Lindroth, 1963; Christensen *et al.*, 1994; McKinnell, 1998, Koljonen, 2001) and fish passage problems at hydropower facilities (Laine, 2002; Rivinoja, 2005). Studies of sea trout population genetics are generally lacking and research on sea trout migration biology and fisheries management is scarce (Jutila *et al.*, 2006; Calles, 2005; ICES, 2006; Lundqvist *et al.*, 2006). Despite large compensatory releases of hatchery juveniles during the last 50 years, studies of the genetic impact of stocking on wild populations are rare (Dannewitz, 2003). Recently, concerns have been raised regarding the poor status of sea trout in the northern Baltic. Milner *et al.* (2006) stated that there is an urgent need to focus on sea trout research as these populations are seriously threatened. Furthermore, Milner *et al.* (2006) underscored the importance of gaining a better understanding of stock structure, the genetic and ecologic consequences of stocking, and the “catchment scale connectivity of habitats, spawning distribution and population dispersal”.

The two rivers Vindelälven and Piteälven entering the Gulf of Bothnia have natural production of both Atlantic salmon and sea trout. They are affected by anthropogenic activities as hydro-electric power production and log floating. Data on fish passes at fish ladders have been monitored the last 30 and 15 year period in the two rivers, respectively. Their history, available background information and the importance of the rivers for the wild anadromous fish in the northern Baltic, makes them suitable for studies of the salmon and sea trout and effects of habitat restorations. The genetic structure of salmon in the northern Baltic is well studied, while the genetic structure of sea trout not has been previously investigated.

Thesis objectives

The overall objectives of this thesis were to study the spawning migration and spawning site selection of sea trout and Atlantic salmon and to analyze the genetic structure of brown trout populations in the northern Baltic Sea area. The thesis focuses on the general biology of the species and aims to describe patterns of variations in migratory behaviour and population genetics and relate those to anthropogenic factors such as habitat alteration and fish stocking. A combination of telemetric and genetic techniques was used to examine following questions:

1. What is the migratory behaviour of sea trout and Atlantic salmon before, during and after spawning in a natural river and what environmental factors affect this behaviour? (Paper II, III and V)
2. Which spawning habitats, i.e. mainstem or tributaries, do sea trout and Atlantic salmon select in two northern river systems and does this vary among species and rivers? (Paper II and III)
3. What are the genetic characteristics of resident and anadromous brown trout in the study rivers? (Paper IV)
4. What ecological and genetic response can be expected by habitat restoration and stocking of fish and are such actions a good strategy for the management of wild salmonid populations? (Paper I, III, IV, VI)

Life history of sea trout and Atlantic salmon

Sea trout and Atlantic salmon in Scandinavia generally ascend rivers and streams for spawning during summer and autumn (see review by Klementsén *et al.*, 2003). The arrival time at river entrance varies with species, population, size and sex (McKinnell *et al.*, 1994; L'Abée-Lund *et al.*, 1989; Jonsson *et al.*, 2001). Accurate timing is important to ensure that the spawning grounds are reached at an appropriate time in maturation schedule. The earliest migrants have been shown to migrate the longest distances to their spawning areas. Their migration behaviour has been described as consisting of two or three phases of migration (e.g. Thorstad, 2006 and references therein).

Spawning habitat preferences differ between sea trout and salmon. Sea trout commonly prefer smaller gravel size and lower water velocities than salmon and are therefore found spawning more often in the smaller tributaries (Bagliniere and Maisse, 1999; Armstrong *et al.*, 2003). Timing of spawning is important and will affect the date of emergence of fry (Brännäs 1988, Elliot & Hurley 1998). Early fry development may lead to increased mortality since the water environment at emergence may be suboptimal. The eggs of anadromous salmonids hatch in spring and the juveniles (smolts) leave their natal stream after one to several years in freshwater for feeding in the sea. Northern Baltic salmon migrate relatively long distances to their feeding areas in the southern Baltic, while sea trout in the Gulf of Bothnia tend to remain in this area (McKinnell, 1997; Lundqvist *et al.*, 2006).

Salmonids generally return to the river where they were hatched, a behaviour known as homing (Stuart, 1957; Quinn, 1993). The ability to home is an important factor responsible for the development of river-specific populations. Juvenile salmonids imprint on the local water chemistry, mainly during seaward migration

as smolts, which they later recognize when returning as adults (Hasler, 1983; Stabell, 1984; Jonsson *et al.*, 1990; Quinn, 1993). Consequently, salmonids that are released as juveniles are generally destined to return to the area of release for spawning even though this may not always be the case (Carlin, 1969; Quinn, 2004). The majority of returning fish home precisely even though a fraction of fish stray to other rivers for upstream migration and spawning (Quinn, 1993; Jonsson *et al.*, 2003). This straying behaviour may be important for evolutionary processes and gives individuals a possibility to colonise new habitats. Both brown trout and Atlantic salmon are iteroparous, so they can survive to contribute their genes to several cohorts (Klemetsen *et al.*, 2003) which is important for sustainability of the species. Among the Pacific salmonids (*Oncorhynchus spp.*) only the steelhead (*Oncorhynchus mykiss*) and cutthroat trout (*Oncorhynchus clarki*) are iteroparous and the common name for salmonid individuals that survive after spawning is kelts (Quinn, 2004).

Material & methods

Study areas

Two mountain rivers, Vindelälven and Piteälven (Figure 1), are classified as Swedish National Rivers. They enter the Gulf of Bothnia in the domain 63–65°N 20–21°E. These rivers are similar in size, water discharge and temperature regime and both have flows regulated in the lower reaches by hydroelectric power production. The Vindelälven, the largest tributary to the river Umeälven, joins 10 km upstream of the power-station Stornorrfor, situated c. 32 km from the coast. On the Piteälven, the Sikfors power-station is situated c. 40 km from the coast. Fish ladders at the dams enable upstream passage of migrating fish. There are no facilities for downstream passage or guidance devices at either of the two hydropower facilities. All anadromous populations of trout and salmon in the Vindelälven gain access to its spawning grounds via the Umeälven. The lowest fish ladders in each river have a trap or camera unit so the number of upstream migrants can be monitored. Counting the number of spawning migrants by species has been done since 1974 and since 1992 for the Vindelälven and Piteälven, respectively. Returning sea trout and salmon ascend the ladders from June–September. The magnitude of the return migration has in general been larger for salmon than sea trout (Figure 2). The average annual spawning run of sea trout has been very low in the rivers Vindelälven and Piteälven with an average of 50 (SD±34) individuals over the latest 30 years (1974–2004) and 98 (SD±50) over the latest 13 years (1992–2004) for the two rivers, respectively (Figure 2). Further details on water flows, temperature, operational information of the power-stations and hatchery production can be found in the thesis papers (I–V). Figure 1 also shows the locations of three smaller forest rivers, Sävarån, Öreälven and Byskeälven, that are studied in paper VI. Sävarån enters the Gulf of Bothnia at c. 40 km north from the Umeälven estuary (Figure 1) and is described in more detail in paper VI.

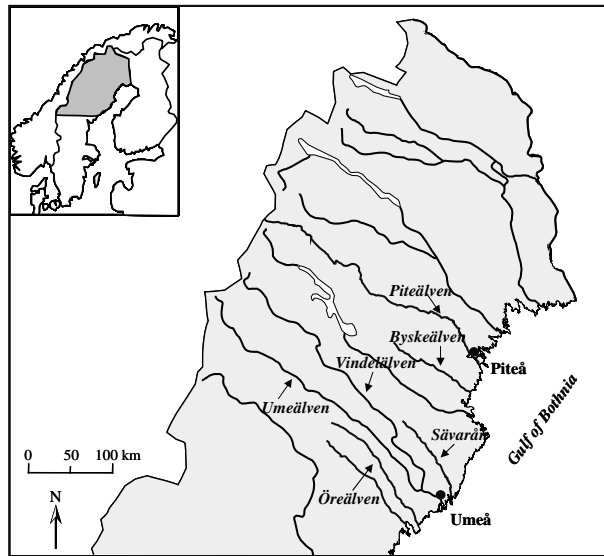


Fig 1. Map over the study area showing the mainstems of the study rivers Vindelälven, Piteälven, Umeälven, Sävarån, Öreälven and Byskeälven in the northern part of Sweden.

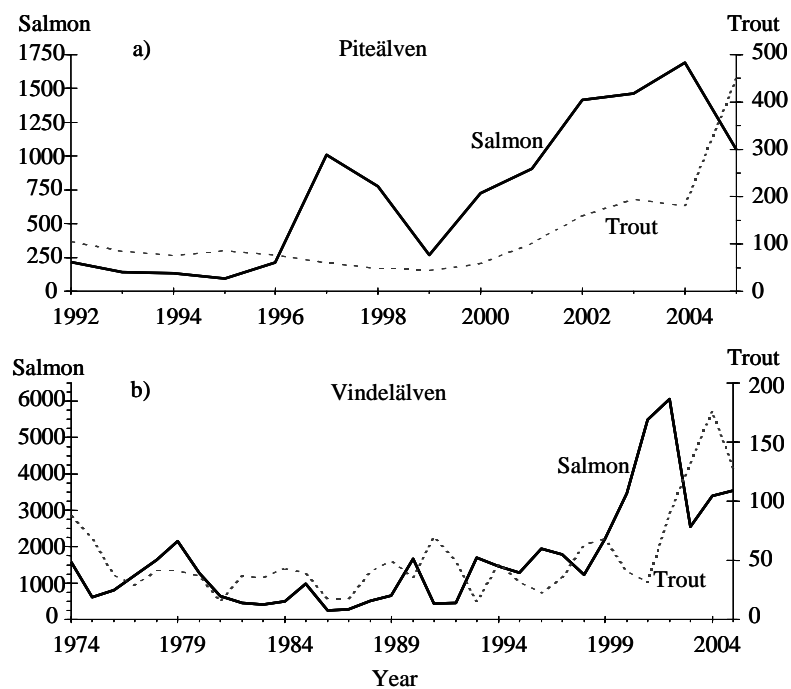


Fig 2. Annual upstream migration of salmon (solid lines) and sea trout (dotted lines) in the fish ladders in Piteälven (a) and Vindelälven (b).

Telemetry

In recent years, research on the migration of fishes has made use of tags that transmit radio or acoustic signals (Cook *et al.*, 2004; Spedicato *et al.*, 2005). This technique collects detailed information on individuals to evaluate fish passages (Calles, 2005; Rivinoja, 2005; Scruton *et al.*, 2006), spawning migration (Økland *et al.*, 2001; Finstad *et al.*, 2005; Arnekleiv & Rønning, 2004), energetics (Thorstad *et al.*, 2000; Hinch *et al.*, 2002) and the downstream migration (Bendall *et al.*, 2005) of adult salmonids. External radio transmitters were used in this thesis (II; III; V) with options to detect activity and mortality signals (III; V). These types of tags are unlikely to have negative effects on fish studies (e.g. Winter, 1996; Brown *et al.*, 1999; Thorstad *et al.*, 2000; Jepsen *et al.*, 2005; Rivinoja, 2005). Only individuals without visible injuries were radio tagged. For detection and tracking of tagged fish, hand held receivers were used when tracking by foot, car, or airplane, and occasionally by boat. Stationary receivers were also installed at fixed locations to provide continuous detection of migrations and movements at these stations. Details of the tagging procedures and receiver calibration and locations appear in thesis papers (II; III; V).

Genetic analyses

Genetic diversity arises from differences in the sequences of nucleotides in the DNA molecule among individuals and it can be measured using genetic markers. Genetic markers have been used to study salmonid populations since the 1960s (Ryman, 1983; Utter, 1991; Ward 2000). The first genetic markers were allozymes, or protein coding loci, followed by mitochondrial DNA (mtDNA) (Ferguson *et al.* 1995; Ward, 2000). mtDNA is considered to be a rather good tool since it is maternally inherited and haploid, making it more sensitive to random genetic drift (Vasemägi 2004 and references therein). At present, microsatellite markers, which are non-coding repeated nucleic DNA sequences, have gained popularity. They are highly variable and widely used both at individual and population level analyses in genetic studies of fish (see review by Chistiakov *et al.*, 2006). In this thesis, tissue samples of brown trout were sampled as the opportunity arose i.e. while radio tagging, trapping, angling and by electro fishing at a number of locations throughout the two watersheds (IV; VI). The genetic diversity and population structure analyses were based on eight microsatellite loci. Extracted DNA was amplified with PCR and further analysed using an automatic sequencer. In paper VI, part of the analysis was made with mtDNA. Details on the laboratory procedures and statistical analyses are specified in the thesis papers (III; IV; VI).

Statistical treatment of data

In the telemetry studies of fish migrations, data from individual sightings and logger data were analysed using the statistical packages SYSTAT and SPSS. Details of the analyses are specified in the thesis papers (II; III; V). The development of genetic analytical methods and statistical programs for population genetics research has improved a great deal the recent years (Waples & Gaggiotti, 2006). In this thesis commonly used methods such as traditional *F*-statistics describing genetic diversity and assignment test with underlying Bayesian statistics were used. Spatial autocorrelation and isolation by distance analysis was also applied.

Software packages used were GENEPOP 3.1 and 3.4 (Raymond & Rousset 1995), POPGENE 1.31 (<http://www.ualberta.ca/~fyeh>). FSTAT 2.9.3 (Goudet, 2001), GENALEX 6 (Peakall & Smouse, 2006), STRUCTURE (Prichard & Wen 2004), BAYES (Pella & Masuda, 2001), GENECLASS 2 (Piry *et al.* 2004), ARLEQUIN 1.1 (Schneider *et al.*, 1997) and POPULATIONS 1.2.28 (Langella, 1999). Analyses are specified in the thesis papers (III; IV; VI).

Results – summary of papers

I.

This paper describes the history of log driving and discusses its impact on physical and biological conditions and stream processes. We review the literature on river restoration to make predictions of the ecological response of log driving. Numerous restorations of river habitats have only recently been done so long term evaluations of the response of river ecology are therefore lacking. In general, rivers that were used as log floatways changed the environmental conditions in the streams abruptly when flow was regulated by dams. Habitat complexity was reduced when boulders were removed, and when reaches were straightened and narrowed. We hypothesized restoration of floatways to increase habitat heterogeneity and stream sinuosity, to improve the land-water interactions and to increase retention capacity of water, sediment, organic matter and nutrients. We suggested that these interventions will favour production, diversity, migration and reproduction of riparian and aquatic organisms. Habitat change and increased connectivity was believed to positively influence brown trout and Atlantic salmon populations. Response rates are expected to vary since some habitat components such as bedrock was destroyed and was believed to be difficult to restore. It may therefore require a long time for change in response variables (e.g. fish abundance) can be detected. Thus, the importance of long term monitoring of biota and continuous evaluation at several scales was emphasized.

II.

The spawning migration of radio-tagged Atlantic salmon females (n=190) ascending the river Vindelälven was studied for three consecutive years, 1997–1999. There was interannual variation in migration speeds and in the amount of time spent resting at specific rapids during the upstream migration. The distance of spawning migrations varied among individuals and between years up to a distance of c. 250 km upstream of the tagging location. No females entered tributaries to spawn. The distance to the spawning site was negatively correlated to tagging date for two of the three years studied. Females that arrived late migrated at a higher speed (c. 25 km/day) than migrants arriving early (c. 8 km/day). Migration speed was negatively correlated to water flow. The migratory pattern was rather uniform among years with females undertaking one rapid upstream migratory phase followed by a holding phase with minor up- and downstream movements at spawning time.

III.

The spawning migration of radio-tagged sea trout (n=126) was studied over a three year duration (2002–2004) in the rivers Vindelälven and Piteälven.

Spawning migration patterns were very variable among individuals, but three different migratory groups could be identified. The first group included the majority of the tagged individuals ($n=34$) demonstrated several up- and downstream migrations with an average distance of 37 km (max-min: 3.6–75 km) in the Vindelälven and 18 km (3.5–55 km) in the Piteälven, during the entire migration period June–September. The second group consisted of individuals with the longest distance to their spawning areas ($n=27$). They migrated upstream in a stepwise manner. The migration of individuals in the third group had a directed upstream migration to the spawning areas ($n=18$). Males generally had a wider searching behaviour in terms of up- and downstream movements, than females. The distance to the spawning area was negatively correlated to tagging date for data pooled over all years in both rivers. In the Vindelälven, spawning areas were located exclusively in the mainstem while in the Piteälven, 74 % of the tagged individuals ascended tributaries to spawn. In the Vindelälven c. 80 % of the tagged fish returned to areas where hatchery-reared sea trout had been released previously. Genetic assignment tests indicated that the majority of radio-tagged individuals in the Piteälven were homing to their natal stream.

IV.

The genetic structure of 685 brown trout from the two river systems Vindelälven and Piteälven was investigated. A global F_{ST} of 0.09 revealed a genetic differentiation among samples. Over all samples, the diversity (H_e) ranged from 0.44 to 0.71, and a total of 79 alleles were found in eight polymorphic microsatellite loci. Anadromous individuals sampled on their spawning migration in the two rivers had low genetic divergence ($F_{ST}=0.02$) and had a similar and relatively high genetic diversity. In the Piteälven drainage, a clearly differentiated subpopulation of sea migrating trout was found in the tributary Sikån. Also, within each watershed, isolated populations above migration barriers or at a long distance from the sea were detected. No overall genetic correlation with geographic distance was noted, however within the Vindelälven drainage, a correlation was observed (Mantel test: $p<0.01$) as was a spatial autocorrelation suggesting genetic similarity within a distance of c. 29 km. Large-scale releases of hatchery-reared sea trout in the river Laisälven (a tributary to Vindelälven) appear to have had little genetic impact. The interactions between resident and anadromous brown trout appear to be complex with generally low differentiation between populations with open migration routes to the sea.

V.

The post-spawning behaviour, survival and overwintering strategy of radio-tagged sea trout kelts was studied in the rivers Vindelälven (2003 and 2004) and Piteälven (2004). The study revealed high (c. 90%) post-spawning and winter survival. The majority (92%) of kelts overwintered in deep sections of the mainstem where movements were limited. Seaward migration was initiated by an increase in water temperature at 4–6°C, independent of flow regime in both rivers in May–June the year after spawning. The dates and water temperatures at seaward migration were similar for the two consecutive years in the Vindelälven. On their downstream migration the kelts encountered hydro-electric stations where the migration was delayed. Passage mortality was 69% and 25% in the

Vindelälven and Piteälven, respectively. Installations of bypass devices to increase the survival of kelts at dams were recommended.

VI.

This study aimed to evaluate the success of longterm stocking of hatchery-reared salmon and sea trout juveniles from foreign populations in the river Sävarån using molecular genetic variation (mtDNA and microsatellites). No information on the pre-stocking genetic composition of salmon and sea trout in Sävarån was available. In two year-classes of salmon smolts, both mtDNA and microsatellite data indicated that the post-stocking genetic composition differed markedly from the donor strain (Byskeälven) and from other Gulf of Bothnia salmon stocks. Analysis using the STRUCTURE program failed to detect any substructuring of salmon within the Sävarån and individual assignment placed no single individual in the donor stock. Sea trout showed overall low differentiation with maximum F_{ST} of 0.033 making analysis more cumbersome than in salmon. Still, sea trout smolts sampled in the Sävarån deviated significantly from potential donor populations and STRUCTURE results, as well as individual assignment, supported that idea that the majority of the sea trout in Sävarån formed a distinct genetic population. Since we were unable to detect genetic contribution from donor stocks in salmon, we concluded that no introgression had occurred. For sea trout, however, with the overlap in genotypes among the sea trout populations some genetic introgression cannot be ruled out.

Discussion

Up- and downstream migration

Radio-tagged Atlantic salmon females in the Vindelälven showed a general migration pattern that included two phases. The first was a period of directed, active upstream migration. The second phase was an inactive holding pattern of behaviour close to the spawning areas (II). Earlier studies have described the spawning migration of Atlantic salmon as occurring in either a two-phase or a three-phase migration pattern (Heggberget *et al.*, 1988a; Webb, 1989; Laughton, 1991; Økland, *et al.*, 2001; Jokikokko, 2002; Karppinen *et al.*, 2004). Where a third phase was evident, it consisted of several up- and downstream movements prior to the holding phase. It was explained as a search behaviour to find suitable spawning grounds. Although the behaviour of fish in the present studies (II) was relatively similar to observations by Økland, *et al.* (2001) and Jokikokko (2002), no searching phase by salmon females was detected before the inactive holding phase. However, certain movements were observed during the spawning period in mid-October indicating searching or mating (II). It was not possible to relate these movements to mating/spawning behaviour since no males were tagged in this study. Thorstad (2006) mentioned that sex-related differences in spawning migration patterns have rarely been noted for Atlantic salmon. Conversely, there were significant sex-related differences in up- and downstream movements in sea trout, where males had a wider search behaviour than females (III). These observations differed from observations by Finstad *et al.* (2005) who did not observe any sex-related differences in migratory behaviour of sea trout.

Finstad *et al.* (2005) did notice a difference between sea trout and Atlantic salmon where sea trout showed a more erratic spawning migration pattern than salmon. In the present studies (II; III) species-specific differences in migration were obvious since salmon showed a more directed and uniform migration to or close to the spawning site than sea trout. Instead, they expressed a variable and erratic migration pattern undertaking several up- and downstream movements (III), in line with the study by Finstad *et al.* (2005) but with much wider movements. The species-specific differences may be explained by the more flexible variability in life history traits of brown trout than salmon and that this also is reflected in migratory behaviour. In addition, homing has been suggested to be more accurate in salmon than brown trout (Baker, 1978). The large distance of up- and downstream migration of sea trout seen in our study rivers (III) and the demonstration that radio-tagged sea trout had a wider search in Vindelälven than in Piteälven is not readily explained. It may have arisen from the greater extent of stocking activities in the Vindelälven than in the Piteälven. The more extensive search behaviour may, to some extent, be related to the hatchery origin of these fish. It has been reported that hatchery reared salmon released as smolts exhibit more up- and downstream movements on their spawning migration as returning adults than wild salmon (Jonsson *et al.* 1991; Jokikokko, 2002). Hence, I expect wild fish to be more precise in their homing than their hatchery counterparts, and if so, the hatchery procedure may affect homing behaviour and induce a wider search reach. The juvenile trout used in the stockings in the Vindelälven were one year old and taken from a brood stock of returning hatchery and wild sea trout caught in the Norrfors fish ladder (Umeälven). The wild individuals in the brood stock may have originated from spawning areas in the lower part of the Vindelälven or high up in the river system. Hence, there was an artificial mixing of genotypes that may be coding for long or short migratory distance. Perhaps this artificial mixing of genotypes affected the migration behaviour. Quinn (2004) suggested that it seems reasonable to assume that there is a genetic component to homing behaviour though it is not fully understood.

The data collected for paper II also indicated a relationship between river steepness and migratory behaviour, which has not been evaluated in other studies. Salmon females aggregated at the steeper sections and lowered their migration speed at increased water flows. Interestingly, the time spent by females during the early spawning migration below the dam in Umeälven (c. 42 days), with an elevation of 72 meters for the first c. 32 km from the sea, was several times longer than the time they spent on migration the following c. 176 km to the fixed automatic receiver (c. 15 days) at an altitude of c. 230 meter above sea level (Rivinoja, 2005; II). The reason for the delay in the lower part of the river is unclear but could be expression of a stock-specific adaptation to “hold and wait” and thus avoid high floods in this steep section of the river. The evolution of such stock-specific characteristics is likely since Atlantic salmon and sea trout inhabit watersheds that differ in size, geographic location, geomorphology, water temperature and flow regimes. Thus, the time of river entry, migration speed and holding location would vary between stocks in different rivers. Latitudinal clines in a number of life history traits as longevity, smolt age and age and size at maturity have been found among sea trout and these life history differences were related to the size of the river (L’Abée-Lund *et al.*, 1989; Jonsson & L’Abée-Lund, 1993; Jonsson *et al.*, 2001). Paper IV revealed that among the radio tagged

sea trout in Piteälven, a group of individuals that ascended the tributary Sikån was genetically distinct. This group was tagged at a significantly earlier date and was observed to migrate a significantly longer distance to spawn compared to other radio-tagged sea trout individuals. Fish migrating upstream to the Sikån also demonstrated a similar migratory behaviour, resting at similar rapids along the river (III). Moreover, the majority (5 of 7) of these individuals held at the Fällforsen rapid, while other tagged individuals, not migrating upstream Sikån, passed Fällforsen without holding. Holding was also observed among the other individuals, however a lesser proportion (8 of 24).

The resting or holding behaviour at rapids (II; III) has been noted by Økland *et al.* (2001) and Karppinen *et al.* (2004) since Atlantic salmon may stop for a couple of days at rapids on their spawning migration. The fish may be recovering from previous periods of migration or holding until the conditions improve to pass a rapid. Water flows and temperatures have a significant impact on the spawning migration of salmon and sea trout (Banks, 1969; Jonsson & Jonsson, 2002; Calles, 2005; Thorstad, 2006; II; III) and high water flow has been observed to delay upstream migrations of salmon and some natural rapids could only be passed at low discharges (Jensen *et al.*, 1986; Rivinoja, 2005). However, increased water flow has also been connected to increased migration speed of salmon (Erkinaro *et al.*, 1999) and has been shown to trigger upstream migration of sea trout (Svendsen *et al.*, 2004). As pointed out by Trepanier *et al.* (1996) there seems to be a lack of consensus of effects of water discharge on salmonid upstream migration. Thus, it seems that the extended period of resting at Fällforsen shown by sea trout ascending Sikån is due to population-specific migratory behaviour.

Temperature may affect fish migration and it has been shown that salmonids may have problems to pass obstacles at temperatures below 5–8°C (Jensen, *et al.*, 1986; Ovidio & Phillipart, 2002). There are few studies of Atlantic salmon and sea trout migrations at high water temperatures above 20°C. In paper III, sea trout that were radio-tagged at temperatures >20° during their upstream migration returned downstream after release at the fish ladder upstream of the power-station and most subsequently died when they entered the water intake to the power-station. The increase in ambient temperature in spring was also considered to be an important factor for the downstream migrations of sea trout kelts in both our study rivers (V). The downstream migration of kelts occurred within the same temperature range that was observed by Jonsson & Jonsson (2002).

Generally, the radio-tagged salmon females in Vindelälven seemed to have arrived on their spawning grounds well in advance of spawning dates. Many studies on the spawning migration of Atlantic salmon report an early arrival at the spawning grounds (Thorstad, 2006 and references therein). The delays in the lower part of the river seen in study II did not, to our knowledge, severely affect spawning activity of the female salmon. Among the radio-tagged sea trout, however, a number of individuals migrated significant distances (>20 km) close to spawning time, in water temperatures <3°C and did not establish holding positions prior to spawning (III). No similar observations have been found described in the literature. This behaviour may have affected reproductive success of these individuals since salmonids may suffer from increased egg mortality due to overripening (de Gaudemar & Beall, 1998) at the end of the spawning period. The high survival post-spawning and high over-winter survival of sea trout suggests that, even after the bioenergetic demands of upstream migration and spawning,

their status in spring was sufficient to undertake seaward migrations in the spring (V). In the Vindelälven, the pre-spawning mortality was higher for long distance migrants that were tagged early in the migration season (III). The spawning and over-winter survival rates of sea trout presented in paper V were higher than reported in other studies, even though winter survival of sea trout kelts rarely have been estimated (Berg & Jonsson, 1990). However, the high mortality of sea trout kelts at passage of the power-stations (III) was likely to have a negative effect on the sea trout populations in these study rivers.

Spawning habitats

The areas selected for spawning differed between the two species in Vindelälven (II; III) and between the two rivers regarding sea trout (III). The salmon had their main spawning area high up in the mainstem of the Vindelälven and the females spawned at similar habitats as reported from other studies (Heggberget *et al.*, 1988b; Armstrong *et al.* 2003). In contrast, most of the sea trout in Piteälven entered various minor tributaries for spawning, as has been shown in studies by Campbell (1977), Elliot (1994) and Bagliniere & Maisse (1999). The sea trout in Vindelälven showed a somewhat different habitat choice than the trout in Piteälven since a majority of these fish spawned in the mainstem, in habitats similar to those used by salmon. However, a few trout entered small side channels for spawning which the salmon never did (II; III). One possible explanation for the trout to select habitat in the mainstem for spawning in Vindelälven may be related to the stocking of hatchery trout in this area. Furthermore, the large numbers of dams built during the log floating era (I) may also have contributed to a loss of migratory populations of trout that used tributaries since migration barriers may induce residency in brown trout populations (Hindar *et al.*, 1991; Northcote 1992).

In accordance with findings by Evans (1994), Bagliniere *et al.* (1990) and Bendall *et al.* (2005), a majority of sea trout and salmon in both study rivers left the spawning area and moved downstream immediately after spawning (II; III; V). This was most obvious for individuals spawning in tributaries (III; V). Again, sea trout in Sikån showed a similar behaviour, leaving the tributary early and undertaking the longest downstream migrations to their winter habitat, compared to other radio-tagged fish in Piteälven. Only a small fraction of sea trout in both study rivers migrated seaward immediately after spawning; the majority overwintered in the rivers. Interestingly, overwintering habitats were noted upstream of the spawning areas in the Vindelälven suggesting that these individuals may have had some previous experience of suitable winter habitats i.e. deep areas covered with ice during the winter (V).

Genetic diversity and genetic structure

The genetic structure and diversity of brown trout (IV) were in accordance with other studies of brown trout (Ryman, 1983; Ferguson, 1989; Hansen & Mensberg, 1998; Carlsson, 2000; Ruzzante *et al.*, 2001; Palm *et al.*, 2003). Thus, the variability and lack of genetic and geographic correlation over large areas were confirmed. Interestingly, the genetic differentiation among sea trout in the two rivers was weak, with the exception of individuals migrating to the river Sikån (IV). These individuals were clearly differentiated as a subpopulation. This

subpopulation structure was an important finding and suggests that similar substructures may exist in other rivers and thus have the need to be conserved.

There seems to be very little gene flow between the population of lake-dwelling trout that spawn downstream of Ammarnäs, high up in Vindelälven, and sea trout, whereas there is clearly some gene flow between resident trout in the tributary Laisälven and sea trout (Andersson, 1988; III; IV). Both the Vindelälven and Laisälven runs through the lake where the lake dwelling trout have their feeding areas, so the differentiation between Ammarnäs and Laisälven was rather unexpected and suggests a relatively strong homing behaviour of the lake-dwelling population to their spawning areas. Ryman *et al.* (1979) and Heggenes *et al.* (2002) also describe clearly differentiated sympatric populations of brown trout feeding in the same lake. Paper IV demonstrated that sea trout populations located above migration barriers were clearly differentiated and had a lower genetic diversity than other brown trout, in accordance with Carlsson (2000) who stressed the importance of migration barriers on population differentiation. Introductions of migration barriers may thus lead to population fragmentation and loss of genetic diversity (Nehlsen, *et al.*, 1991; Hindar *et al.*, 2001; Gosset, *et al.* 2006). It is therefore likely that floatway constructions in the study river systems may have had an effect on the genetic structure of the brown trout. Nevertheless, a genetic response takes time and even though no radio-tagged individuals entered any tributary for spawning in the Vindelälven, the recent removal of log floating dams and re-establishment of the connectivity in the river makes gene flow between different trout population possible. The low genetic differentiation and isolation by distance among populations in the Vindelälven, after excluding outlier populations, also suggests relatively high gene flow. Moran *et al.* (1995) and Ferguson *et al.* (1995) suggested that gene flow is higher among rivers supporting sea trout than among resident brown trout populations. In addition, Ferguson *et al.* (1995) found that sea trout populations are genetically more variable than resident populations. This was also the case in study (IV) where the highest genetic diversity was found in sea trout populations from Vindelälven and Piteälven. Furthermore, paper (VI) revealed weak genetic differences between additional sea trout populations in the Gulf of Bothnia. This is consistent with the idea that anadromous trout are not particularly committed to homing to natal rivers. The nature of the interactions between resident and anadromous individuals remains unclear, even though the presence of sea trout in a river has the potential to increase gene flow from other rivers.

Salmon and sea trout in the Vindelälven and sea trout in the Piteälven migrated upstream in these river systems and selected an area for spawning. Paper III and IV give genetic as well as radio-tracking support to that sea trout are homing to certain tributaries within the two watersheds. Trout homing to the same stream, or tributary, is well known and homing is believed to be one important underlying factor contributing to the genetic population structure among both salmon and brown trout (Stuart, 1957; Laikre *et al.* 1999 and references therein, Carlsson & Nilsson, 2001; Quinn, 2004; Primmer *et al.*, 2006). Salmon and brown trout that are experimentally displaced will usually return to previously established positions in the river (Heggberget *et al.*, 1988a, Armstrong & Herbert 1997). In contrast, Carlsson *et al.* (1999) failed to find any genetic support for homing where displaced brown trout had returned to previously established locations (Halvorsen & Stabell, 1990).

Habitat restoration, stocking & management

Humans have altered the natural courses of rivers and streams and used the power of the water for log floating, milling, and production of electricity. This has had an effect on the production and diversity of aquatic and riparian organisms in the majority of streams in Sweden (I). Floatway constructions lead to a decrease in connectivity and deterioration of spawning habitat and rearing areas (Jutila *et al.*, 1998; Scruton *et al.*, 1998; I). Recently, the importance of habitat restoration has gained interest in Sweden and a goal of these restoration efforts is often to increase fish production. Overall, float way restorations lead to a positive response by the riparian forest production, an increased retentiveness of coarse particulate organic matter and increased habitat complexity which tends to increase food abundance for fish (Lepori *et al.*, 2005; I). Fish biomass and species diversity are increased after floatway restoration mainly due to an increase in wetted area (Lepori *et al.*, 2005; Palm, 2006 pers. comm). Reconstruction of spawning habitat generally increases abundance of brown trout juveniles (Stridsman, 1995; Daniel Palm pers. comm.). It has been shown that brown trout juveniles can outcompete salmon juveniles at lower water velocities and should therefore respond more favourably than salmon after restoration since the kinds of restorations occurring in the northern Swedish rivers will often reduce water velocity (Heggenes and Saltveit, 1990; I). Näslund (1989) and Chapman (1966) suggested that salmonid juveniles would experience higher survival rates during winter if there was an increased availability of pools as a consequence of log floating restorations. In addition, it may be expected that restoration of small tributaries might have a greater impact on the habitat than restorations in the mainstem, a result that would also favour sea trout that prefer smaller streams and tributaries for reproduction (III).

The removal of dams and stone piers facilitate migration by salmonids, according to our observations of one radio tagged individual in Piteälven that passed a newly restored area; unfortunately, it was unable to pass an unrestored area that was located further upstream (III). However, the response of all organisms is often ecologically connected and other factors such as fishing and water power production can influence the migration of anadromous salmonids. As stressed in paper V, it is important to create migration passes both up- and downstream of dams to ensure the long-term sustainability of salmon and sea trout. Moreover, restored connectivity facilitates gene flow which seems to be important in rivers with sea migrating and resident brown trout (IV).

Stocking salmonids is a common practice throughout Sweden (Laikre *et al.*, 2006). In the Baltic region, the compensatory releases of hatchery fish have been considered an important part of a conservation policy for salmon and sea trout (Lindroth, 1963; McKinnell, 1998; Jonsson, 2001). The practice is also used as a restoration strategy to re-establish populations. This thesis suggests that there have been limited effects of stocking salmon and sea trout in the rivers Sävarån and Laisälven (IV, VI). Paper VI demonstrates that no genetic impact of salmon stocking was detected after 17 years of stocking. In a study of a Norwegian lake, evidence of genetic introgression was not found even after 40 years of stocking of brown trout (Heggenes *et al.* 2002). Similar results have been reported when stocking sea trout (Ruzzante *et al.*, 2004), however, in these studies only domesticated trout were used for stocking. Conversely, Palm *et al.* (2003) reported

that gene flow could be as high as 80% per generation from stocked sea trout of hatchery origin to wild sea trout, when using local parental stock of hatchery sea trout. It has been argued that this kind of supportive breeding may lead to inbreeding and also loss of genetic variation (Ryman & Laikre, 1991; Wang & Ryman, 2001). A reason for the lack of success in stocking some locations may be that the released fish are lacking river-specific characteristics important for survival or reproductive success. In addition, stocking of anadromous populations may also be problematic because of their complex life histories. Quinn (2004) mentioned numerous attempts and failures to establish Pacific salmon stocks by transplanting to rivers that already support populations of the same species. There are examples where re-colonisation without stocking may be fast and successful both by wild salmon and sea trout (Knutsen *et al.*, 2001; Vasemägi *et al.*, 2004) so stocking may not be necessary. It is important to consider time scales when evaluating the effect of habitat restorations and stockings. Habitat restoration may have an immediate effect on complexity, retention and water flow, while the response of biotic organisms may take decades or even centuries. In present studies (IV; VI) stockings were performed until recently and additional investigations are needed to evaluate future genetic impact of these stockings.

A widely used application of genetic data in the management of a species or a population is to define evolutionary significant units (ESU). An ESU may be defined as a population or group of populations that merit a separate management or conservation strategy (Allendorf & Luikart, 2007). Several definitions of an ESU have been suggested based on genetic data, ecologic data or a combination of both types of information (Ryder, 1986; Moritz, 1994; Waples, 1995; Crandall *et al.*, 2000). ESUs are often divided into management units (MU). The MUs should represent different populations, or stocks, that are demographically separated and important for the long-term viability of the whole ESU. It has been stressed that the conservation of multiple populations is vital for the conservation of a species (Allendorf & Luikart, 2007). Also, estimates of interaction and dispersal rates between populations are crucial for an adequate management strategy (Palsbøll *et al.*, 2007). This thesis revealed that the differentiation among sea trout populations in the Gulf of Bothnia is weak and much weaker compared to the differentiation among salmon populations in the same area. Since genetic similarities between sea trout in these rivers suggests that ESUs of sea trout in the Gulf of Bothnia may include a larger number of populations than ESUs of salmon. However, the ESUs should consist of MUs which are based on population structures among and within river systems and should also consider demographic data.

The long-term use of rivers for timber floating and hydropower development threatens the existence of the wild salmon and sea trout in the Baltic Sea and the Gulf of Bothnia (ICES, 2006; I). High exploitation in the open sea fisheries and by-catch in the whitefish fishery have put strong pressure on the wild stocks (ICES, 2006). To safeguard the few remaining stocks of wild salmonids remaining in the Baltic Sea and the Gulf of Bothnia, criteria need to be established that will permit the coexistence of sea trout and salmon; comprehensive river-management programs are needed. Severely reducing the total catch of salmon in the sea would also be a biologically important management strategy for the future conservation of the wild salmon stocks. The same way of thinking would be valid if the coastal- or river fishery overexploit the sea trout and salmon resource.

Concluding remarks and future research needs

In this thesis I have demonstrated inter- and intraspecific variability in migratory behaviour and spawning habitat preference of sea trout and Atlantic salmon. I have found a genetic subpopulation structure within and weak differentiation among sea migrating trout populations and limited genetic introgression from stocked populations. Based on this I emphasize:

- Additional research on salmonid migrations in natural river systems should focus on kelt migration, i.e. help surviving spawners to reach the sea. Even though international research on fish migration at man-made barriers and power-stations recently has received considerable attention, migration studies in natural environments are few. The kelts are very important since repeat spawning involves genetic contribution to several generations. The kelts are especially important in weak populations with high proportions of repeat spawners.
- Additional research on genetic population structure of sea migrating trout with special consideration to the Gulf of Bothnia. This information is generally lacking and genetic diversity, i.e., variation in the genome among individuals as well as among populations, is the basis of evolution and important for the resilience of the native stocks to future changes in the environment. Thus, identification and conservation of genetically differentiated subpopulations is important for management of the sea trout and salmon stocks and could also be used to define ESUs (Evolutionary significant units) or management units.
- More restoration of river habitats, increasing connectivity, and less supplemental stockings of hatchery fish. Management strategies should be focused on allowing the original populations to return as adults to suitable spawning and rearing habitats and to ensure their safe up- and down passage at power-stations. This will, in the long run, increase and strengthen wild salmonid populations. Nevertheless, stocking is still widely performed and there is a need for further research on the effects of stocking, from a genetic and ecologic perspective. Therefore, longterm monitoring programs with genetic sampling should be initiated.

Swedish summary – svensk sammanfattning

Östergren, J. 2006. Migration and Genetic Structure of *Salmo salar* and *Salmo trutta* in Northern Swedish Rivers. Doctor's dissertation. ISSN: 1652-6880. ISBN: 91-576-7261-X.

Denna avhandling undersöker och beskriver vandringsbeteende hos lax och havsöring i de två nationalälvarna Vindelälven och Piteälven, före, under och efter leken, samt hur habitat och miljöfaktorer som vattentemperatur och vattenflöde påverkar detta beteende. Genetisk struktur hos öring i älvarna och genetisk inblandning av utsatta lax- och öringungar utvärderas. Vandrings- och lekplatser, val av lekplats och genetiska resultat relateras också till mänsklig påverkan som skett i vattendragen i samband med flottningsepoken och vattenkraftutbyggnad.

Radiomärkta laxar ($n=128$) och havsöringar ($n=86$) vandrade med olika vandringsmönster innan leken där lax hade ett mer direkt, riktat vandringsbeteende mot sin lekplats än havsöring som istället simmade långa sträckor upp- och nedströms under hela lek- och vandringsperioden. Vandringshastigheten var lägre vid forspartier i älvarna och minskade med ökat vattenflöde. Fiskar som vandrade sent på säsongen var snabbare (25 km/dygn) än de som vandrade tidigt (8 km/dygn). De tidigt stigande fiskarna hos båda arterna vandrade också längsta sträcka till sin lekplats. I Vindelälven lekte lax och havsöring i huvudfåran, ca. 230 respektive 60 km uppströms i älven, medan havsöringen i Piteälven lekte i ett antal biflöden. Huvuddelen, ca. 90 %, av havsöringarna överlevde leken och övervintrade i älvarnas huvudfåror. De vandrade nedströms mot havet följande vår i stigande vattentemperaturer på 4–6°C. En dödlighet av 69% och 25% noterades vid passage av vattenkraftverk för fiskarna som lekte i Vindel- respektive Piteälven.

Genetiska analyser visade på en stor differentiering mellan öringpopulationer med olika livshistoria i de båda vattensystemen ($F_{ST}=0.09$). Differentiering mellan havsöringpopulationer i älvarna, inkluderat Sävarån och Öreälven, visade sig däremot vara svag (maximum $F_{ST}=0.03$). Det fanns inget samband mellan genetisk och geografisk distans, däremot fanns ett sådant samband inom Vindelälven, så att det genetiska avståndet ökade med geografiskt avstånd. I Piteälven upptäcktes en delpopulation av havsvandrande öring som lekte i biflödet Sikån. Genetiskt assignment visade, tillsammans med resultat från pejling av radiomärkt fisk, att havsöringar från denna delpopulation vandrade till sitt hemvattendrag. Trots utsättningar av laxungar från främmande populationer, i huvudsak Byskeälvslox, under 17 år i Sävarån, kunde inte någon genetisk inblandning från de utsatta fiskarna noteras. Även havsöring av främmande härkomst, från Vindelälven och Öreälven, har frisläppts i Sävarån. Stora genetiska likheter mellan havsöring i dessa älvar och Sävarån, gjorde dock att det var svårare att avgöra om det skett någon genetisk inblandning av den utsatta fisken. Det konstateras att Sävarån har egna unika populationer av både lax och havsöring.

Habitatrestering samt återskapande av fria vandringsvägar predikteras öka produktionen av lax och havsöring samt underlätta förutsättningar för genflöde mellan populationer av öring. Det är också viktigt för de vilda populationernas fortsatta överlevnad och för en positiv utveckling av resursen vandringsfisk.

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References

- Allendorf, F. W. & Luikart, G. 2007. *Conservation and the genetics of populations*. ISBN-3: 978-1-4051-2145-3 Blackwell Publishing. Malden, USA.
- Andersson, T. 1988. Havsöring. Fiskeristyrelsen Utredningskontoret, Härnösand.
- Armstrong, J.D & Herbert, N.A. 1997. Homing movements of displaced stream-dwelling brown trout. *Journal of Fish Biology*. 50, 445-449.
- Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M. & Milner, N.J. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research* 62, 143-170.
- Arnekleiv, J.V. & Ronning, L. 2004. Migratory patterns and return to the catch site of adult brown trout (*Salmo trutta* L) in a regulated river. *River Research and Applications* 20, 929-942.
- Bagliniere, J.L. & Maisse, G. 1999. *Biology and ecology of the brown and sea trout*, Springer, ISBN 1-85233-117-88, Chester, UK
- Bagliniere, J.-L., Maisse, G. & Nihouarn, A. 1990. Migratory and reproductive behaviour of female adult Atlantic salmon, *Salmo salar* L., in a spawning stream. *Journal of Fish Biology* 36, 511-520.
- Baker, R.R. 1978. *The evolutionary ecology of animal migration*. London: Hodder & Stoughton.
- Banks, J.W. 1969. A review of the literature on the upstream migration of adult salmonoids. *Journal of Fish Biology* 1, 85-36.
- Bendall, B., Moore, A. & Quale, V. 2005. The post-spawning movements of migratory brown trout *Salmo trutta* L. *Journal of Fish Biology* 67, 809-822.
- Berg, O.K. & Jonsson, B. 1990. Growth and survival rates of the anadromous trout, *Salmo trutta*, from the Vardenes River, northern Norway. *Environmental Biology of Fishes* 29, 145-154.
- Brown, R.S., Cooke, S.J., Anderson, W.G., McKinley, R.S. 1999. Evidence to Challenge the "2%Rule" for Biotelemetry. *North American Journal of Fisheries Management* 19: 867-871
- Brännäs, E. 1988. Emergence of Baltic salmon, *Salmo salar* L., in relation to temperature: A laboratory study. *Journal of Fish Biology*. 33(4), 589-600.
- Byström, C. 1868. Om fisket i Umeå elf och skärgård. (In Swedish). - Landtbr-Akad Tidskr: 91-100. Sweden.
- Calles, O. 2005. *Re-establishments of connectivity for fish populations in regulated rivers*. Doctoral thesis. Karlstad University Studies. 2005:56 ISBN: 91-7063-028-3. Karlstad.
- Campbell, J.J. 1977. Spawning characteristics of brown trout and sea trout *Salmo trutta* L. in Kirk Burn, River Tweed, Scotland. *Journal of Fish Biology*. 11, 217-229.
- Carlin, B. 1969. The migration of salmon. Report LFI Medd. 4/1969.
- Carlsson, J. & Nilsson, J. 2001. Effects of Geomorphological Structures on Genetic Differentiation among Brown Trout Populations in a Northern Boreal River Drainage. *Transactions of the American Fisheries Society* 130, 36-45.
- Carlsson, J. 2000. *Population genetic structure of brown trout in boreal ecosystems*. Doctoral thesis: ISSN 1401-6230, ISBN 91-576-5884-6, Swedish University of Agricultural Sciences, Umeå, Sweden.
- Carlsson, J., Olsen, K.H., Nilsson, J., Overli, O. & Stabell, OB. 1999. Microsatellites reveal fine-scale genetic structure in stream-living brown trout. *Journal of Fish Biology*. 55, 1290-1303.
- Chapman, D.W. 1966. Food and space as regulators of salmonid populations in streams. - *American Naturaliste* 100, 345-357.
- Chistiakov, D.A., Hellemans, B. & Volckaert, F.A.M. 2006. Microsatellites and their genomic distribution, evolution, function and applications: A review with special reference to fish genetics *Aquaculture* 255(1-4), 1-29.
- Christensen, O., Eriksson, C. & Ikonen, E. 1994. History of the Baltic salmon, fisheries and management. In Anonymous. Ninth ICES Dialogue Meeting "Atlantic salmon: A Dialogue". ICES Coop. Res. Rep. No. 197.

- Cooke, S.J., Thorstad, E.B. & Hinch, S.G. 2004. Activity and energetics of free-swimming fish: insights from electromyogram telemetry. *Fish and Fisheries* 5, 21-52.
- Crandall, K.A., Bininda-Emonds, O.R.P., Mace, G.M., Wayne, R.K., 2000. Considering evolutionary process in conservation biology. *Trends in Ecology and Evolution*. 15, 290-295.
- Dannewitz, J. 2003. *Genetic and ecological consequences of fish releases*. Doctoral thesis. Faculty of science and technology 906 Uppsala University. ISSN 1104-232X, ISBN 91-554-5796-7. Uppsala, Sweden.
- de Gaudemar, B. & Beall, E. 1998. Effects of overripening on spawning behaviour and reproductive success of Atlantic salmon females spawning in a controlled flow channel. *Journal of Fish Biology* 53, 434-446.
- Degerman, E., Nyberg, P., & Sers, B. 2001. Havsöringens Ekologi. – Finfo 2001:1, Fiskeriverket. (In Swedish).
- Elliott, J.M. & Hurley, M.A. 1998. An individual-based model for predicting the emergence period of sea trout fry in a Lake District stream. *Journal of Fish Biology*. 53, 414-433.
- Elliott, J.M. 1994. *Quantitative Ecology and the Brown Trout*. Oxford: Oxford University Press.
- Erkinaro, J., Økland, F., Moen, K., Niemelä, E. & Rahiala, M. 1999. Return migration of Atlantic salmon in the River Tana: the role of environmental factors. *Journal of Fish Biology* 55, 506-516.
- Evans, D.M. 1994 Observations on the spawning behaviour of male and female adult sea trout, *Salmo trutta* L., using radio-telemetry. *Fisheries Management and Ecology* 1, 91-105
- Ferguson, A. 1989. Genetic differences among brown trout, *Salmo trutta*, stocks and their importance for the conservation and management of the species. *Freshwater Biology*, 21, 35-46.
- Fergusson, A., Taggart, J.B., Prodöhl, P.A., MvMeel, O., Thompson, C., Stone, C., McGinnity, P. & Hynes, R.A. 1995. The application of molecular markers to the study and conservation, of fish populations, with special reference to *Salmo*. *Journal of Fish Biology* 47, 103-126.
- Finstad, A.G., Økland, F., Thorstad, E.B. & Heggberget, T.G. 2005. Comparing upriver spawning migration of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*. *Journal of Fish Biology* 67, 919-930.
- Garcia-Marin, J.L., Utter, F. & Pla, C. 1999. Postglacial colonization of brown trout in Europe based on distribution of allozyme variants. *Heredity*, 82, 46-56.
- Gosset, C., Rives, J. & Labonne, J. 2006. Effect of habitat fragmentation on spawning migration of brown trout (*Salmo trutta* L.). *Ecology of Freshwater fish* 15, 247-254.
- Goudet, J. 2001. Fstat, a program to estimate and test gene diversities and fixation indices. (version 2.9.3). Université de Lausanne, Dorigny, Switzerland. Available from <http://www2.unil.ch/popgen/softwares/fstat.htm>
- Halvorsen, M. & Stabell, O.B. 1990. Homing behaviour of displaced stream-dwelling brown trout. *Animal Behaviour* 39, 1089-1097.
- Hansen, M.M. & Mensberg, K.L. 1998. Genetic differentiation and relationship between genetic and geographic distance in Danish sea trout (*Salmo trutta* L.) populations. *Heredity*. 81, 493-504.
- Hasler, A.D. 1983. Olfactory imprinting and homing in salmon: Investigations into the mechanism of the imprinting process. *Zoophysiology* 14
- Heggberget, T.G., Hansen, L.P. & Næsje, T.F. 1988a. Within-river spawning migration of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 45, 1691-1698.
- Heggberget, T.G., Haukebö, T., Mork, J. and Ståhl, G. 1988b. Temporal and spatial segregation of spawning in sympatric populations of Atlantic salmon, *Salmo salar* L, and brown trout, *Salmo trutta* L. *Journal of Fish Biology* 33, 347-356.
- Heggenes, J., Roed, K.H., Hoeyheim, B. & Rosef, L. 2002. Microsatellite diversity assessment of brown trout (*Salmo trutta*) population structure indicate limited genetic impact of stocking in a Norwegian alpine lake. *Ecology of Freshwater Fish*. 11(2), 93-100.

- Hinch, S.G., Standen, E.M., Healey, M.C. & Farrell, A.P. 2002. Swimming patterns and behaviour of upriver-migrating adult pink (*Oncorhynchus gorbuscha*) and sockeye (*O. nerka*) salmon as assessed by EMG telemetry in the Fraser River, British Columbia, Canada. *Hydrobiologia* 483, 147-160.
- Hindar, K., Jonsson, B., Ryman, N. & Staahl, G. 1991. Genetic relationships among landlocked, resident, and anadromous brown trout, *Salmo trutta* L. *Heredity*. 66, 83-91.
- Hvarfner, H. 1965. *Hunting and fishing* : Nordic symposium on life in a traditional hunting and fishing milieu in prehistoric times and up to the present day. Luleå, Sweden
- ICES. 2006. Report of the Baltic Salmon and Trout Assessment Working Group (WGBAST), 28 March - 6 April 2006, ICES Headquarters. ICES CM 2006/ACFM:21. 209 pp.
- Jensen, A.J., Heggberget, T.G. & Johnsen, B.O. 1986. Upstream migration of adult Atlantic salmon, *Salmo salar* L., in the River Vefsna, northern Norway. *Journal of Fish Biology* 29, 459-465.
- Jepsen, N., Schreck, C., Clements, S. & Thorstad, E.B. 2005. A brief discussion on the 2% tag/bodymass rule of thumb. In *Aquatic telemetry: advances and applications*, Spedicato MT, Lembo G, Marmulla G (eds). Rome, FAO/COISPA; 255-259.
- Jokikokko, E. 2002. Migration of wild and reared Atlantic salmon (*Salmo salar* L.) in the river Simojoki, northern Finland. *Fisheries Research* 58, 15-23.
- Jokikokko, E. 2002. Migration of wild and reared Atlantic salmon (*Salmo salar* L.) in the river Simojoki, northern Finland. *Fisheries Research* 58, 15-23.
- Jonsson, B. & Jonsson, N. 2002. Migration of anadromous brown trout *Salmo trutta* in a Norwegian river. *Freshwater Biology* 47, 1391-1401
- Jonsson, B. & Jonsson, N. 2006. Life History of the Anadromous Trout *Salmo trutta*. In: *Sea trout: Biology, Conservation and Management*, Harris G, Milner N (eds). Chapter 14. ISBN: 1405129913. Blackwell Publishing Ltd, Oxford, UK.
- Jonsson, B. & LÁbeé-Lund, J.H. 1993. Latitudinal clines in life-history variables of anadromous brown trout in Europe. *Journal of Fish Biology* 43, 1-16.
- Jonsson, B. 1985. Life history patterns of freshwater resident and sea-run migrant browntrout in Norway. *Transactions of the American Fisheries Society* 114, 182-194.
- Jonsson, B. 1989. Life history and habitat use of Norwegian brown trout (*Salmo trutta*). *Freshwater Biology* 21, 71-86.
- Jonsson, B., Jonsson, N. & Hansen, L.P. 1990. Does juvenile experience affect migration and spawning of adult Atlantic salmon? *Behavioural Ecology and Sociobiology* 26, 225-230.
- Jonsson, B., Jonsson, N. & Hansen, L.P. 1991. Differences in life history and migratory behaviour between wild and hatchery-reared Atlantic salmon in nature. *Aquaculture* 98: 69-78.
- Jonsson, B., Jonsson, N. & Hansen, L.P. 2003. Atlantic salmon straying from the River Imsa. *Journal of Fish Biology*. 62, 641-657.
- Jonsson, B., Jonsson, N., Brodtkorp, E. & Ingebrigtsen, P. 2001. Life-history traits of Brown Trout vary with the size of small streams. *Functional Ecology* 15, 310-317.
- Jonsson, N. 1991. Influence of water flow, water temperature and light on fish migration in rivers. *Nordic Journal of Freshwater Research* 66, 20-35.
- Jonsson, S. 2001. *Stocking of Brown Trout (Salmo trutta L.): Factors affecting survival and growth*. Doctoral thesis. Department of aquaculture, SLU, Umeå ISSN 1401-6230 ISBN 91-576-6314-9 Umeå, Sweden.
- Jutila, E., Ahvonen, A., Laamanen, M. & Koskiniemi, J. 1998. Adverse impact of forestry on fish and fisheries in stream environments of the Isojoki basin, western Finland. *Boreal Environment Research*. 3, 395-404.
- Jutila, E., Saura, A., Kallio-Nyberg, I., Huhmarniemi, A. & Romakkaniemi, A. 2006. The Status of Fishing of Sea Trout on the Finnish Coast of the Gulf of Bothnia in the Baltic Sea: In: *Sea trout: Biology, Conservation and Management*, Harris G, Milner N (eds). Chapter 10. ISBN: 1405129913. Blackwell Publishing Ltd, Oxford, UK.
- Karppinen, P., Erkinaro, J., Niemelä, E., Moen, K. & Økland, F. 2004. Return migration of one-sea-winter Atlantic salmon in the River Tana. *Journal of Fish Biology* 64, 1179-1192.

- Klemetsen, A., Amundsen, P.-A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F. and Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish* 12: 1-59.
- Knutsen, H., Knutsen, J.A. & Jorde, P.E. 2001. Genetic evidence for mixed origin of recolonized sea trout populations. *Heredity* 87, 207-214.
- Koljonen, M. 2001. Conservation goals and fisheries management units for Atlantic salmon in the Baltic Sea area. *Journal of Fish Biology* 59, 269-288.
- LÁbeé-Lund, J.H., Jonsson, B., Jensen, A.J., Sættem, L.M., Heggberget, T.G., Johnsen, B.O. & Naesje, T.F. 1989. Latitudinal variation in life-history characteristics of sea-run migrant brown trout *Salmo trutta*. *Journal of Animal Ecology* 58, 525-542.
- Laikre, L. ed. 1999. Conservation Genetic Management of Brown Trout (*Salmo trutta*) in Europe. Report by the Concerted action on identification, management and exploitation of genetic resources in the brown trout (*Salmo trutta*) ("TROUTCONCERT"; EU FAIR CT97-3882).
- Laikre, L., Palmé, A., Josefsson, M., Utter, F. & Ryman, N. 2006. Release of alien populations in Sweden. *Ambio*, 35, 255-261.
- Laine, A., Jokivirta, T. & Katapodis, C. 2002. Atlantic salmon, *Salmo salar* L., and sea trout, *Salmo trutta* L., passage in a regulated northern river - fishway efficiency, fish entrance and environmental factors. *Fisheries Management and Ecology* 9, 65-77.
- Langella, O. 1999. Populations 1.2.28. Available at [http:// www.pge.cnrs-gif.fr/bioinfo/populations/index.php](http://www.pge.cnrs-gif.fr/bioinfo/populations/index.php).
- Laughton, R. 1991. The movements of adult Atlantic salmon in the River Spey as determined by radio telemetry during 1988 and 1989. *Scottish Fisheries Research Report* 50, 1-35.
- Lepori, F., Palm, D. & Malmqvist, B. 2005. Effects of stream restoration on ecosystem functioning: detritus retentiveness and decomposition. *Journal of Applied Ecology* 42, 228-238.
- Lindroth, A. 1963. Salmon conservation in Sweden. *Transaction of the American Fisheries Society* 92, 286-91.
- Lindroth, A. 1965. Baltic salmon stock: its natural and artificial regulation. *Mitt. Internat. Verein. Limnol* 13, 163-192.
- Lundqvist, H., McKinnell, S.M., Jonsson, S. & Östergren, J. 2006. Are Reared Anadromous Brown trout Compatible with the Conservation of Wild Trout ?, In : *Sea Trout, Biology, Conservation & Management*. Eds: G. Harris & N. Milner. Fishing News Books, Blackwell Scientific Publications, 2006. ISBN 1405129913. Oxford, UK.
- McKinnell, S.M. 1997. A Retrospective on Baltic Salmon (*Salmo salar* L.) Biology and Fisheries. *Nordic Journal of Freshwater Research* 73, 73-88.
- McKinnell, S.M. 1998. Atlantic salmon (*Salmo salar* L.) life history variation: implications for the Baltic Sea fishery. Doctoral thesis, Swedish University of Agricultural Sciences. ISSN ISBN: Umeå Sweden
- McKinnell, S.M., Lundqvist, H. Johansson, H. 1994. Biological characteristics of the upstream migration of naturally and hatchery-reared Baltic salmon, *Salmo salar* L. homing and straying in salmon. *Aquaculture fisheries and management*, 25, Suppl. 2. 46-63.
- Milner, N.J., Harris, G.S., Gargan, P., Beveridge, M., Pawson, M.G., Walker, A. & Whelan, K. 2006. Perspectives on sea trout and management. In Harris, G.S. & Milner, N.J. (eds) *Sea trout: Biology, Conservation and Management*, Proceedings of First International Sea Trout Symposium, Cardiff, July 2004. Fishing News Books, ISBN: 1405129913. Blackwell Scientific Publications, Oxford, 496pp.
- Morán, P., Pendás, A.M., García-Vásquez, E., Izquierdo, J. 1995. Estimates of gene flow among neighbouring populations of brown trout. *Journal of Fish Biology*. 46, 593-602.
- Moritz, C., 1994. Defining evolutionary significant units for conservation. *Trends in Ecology and Evolution* 9, 373-376.
- Nehlsen, W., Williams, J.E. & Lichatowich, J.A. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16, 4-21.

- Nilsson, C., F. Lepori, B. Malmqvist, E. Törnlund, N. Hjerdt, J. M. Helfield, D. Palm, J. Östergren, R. Jansson, E. Brännäs & Lundqvist, H. 2005. Forecasting environmental responses to restoration of rivers used as log floatways: an interdisciplinary challenge. *Ecosystems* 8, 779-800.
- Nilsson, J. Gross, R., Asplund, T., Dove, O., Jansson, H., Kelloniemi, J., Kohlmann, K., Löytynoja, A. Nielsen, E.E., Paaver, T., Primmer, C.R., Titov, S., Vasemägi, A., Veselov, A., Öst, T. & Lumme, J. 2001. Matrilinear phylogeography of Atlantic salmon (*Salmo salar* L.) in Europe and postglacial colonisation of the Baltic Sea area. *Molecular Ecology* 10, 89-102.
- Northcote, T.G. 1992. Migration and residency in stream salmonids - some ecological considerations and evolutionary consequences. *Nordic Journal of Freshwater Research* 67, 5-17.
- Näslund, I. 1989. Effects of habitat improvement on the brown trout, *Salmo trutta* L., population of a northern Swedish stream. - *Aquacult Fish Manage* 20, 463-74.
- Ovidio, M. & Philippart, J.-C. 2002. The impact of small physical obstacles on upstream movements of six species of fish. *Hydrobiologia* 483, 55-69.
- Palm, D. 2006. Department of Aquaculture, SLU, Umeå, Sweden. Personal communication.
- Palm, S., Dannewitz, J., Järvi, T., Petersson, E., Prestegard, T. & Ryman, N. 2003. Lack of molecular genetic divergence between sea-ranched and wild sea trout (*Salmo trutta*). *Molecular Ecology* 12, 2057-2071.
- Palsbøll, P.J., Bérubé, M. & Allendorf, F.W. 2007. Identification of management units using population genetic data. *Trends in Ecology and Evolution*, In press.
- Peakall, R. & Smouse, P.E. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 6, 288-295.
- Pella, J. & Masuda, M. 2001 Bayesian methods for analysis of stock mixtures from genetic characters. *Fishery Bulletin* 99, 151-167.
- Piry, S., Alapetite, A., Cornuet, J.-M., Paetkau, D., Baudouin, L., & Estoup, A. 2004. GeneClass2: A Software for Genetic Assignment and First-Generation Migrant Detection. *Journal of Heredity* 95, 536-539.
- Primmer, C.R., Veselov, A.J., Zubchenko, A., Poututkin, A., Bakhmet, I. & Koskinen, M.T. 2006. Isolation by distance within a river system: genetic population structuring of Atlantic salmon, *Salmo salar*, in tributaries of the Varzuga River in northwest Russia. *Molecular Ecology* 15, 653-666.
- Pritchard, J. & Wen, W. 2004. Documentation for STRUCTURE software: version 2. Available from <http://pritch.bsd.uchicago.edu>.
- Quinn, T. 1993. A review of homing and straying of wild and hatchery produced salmon. *Fisheries research* 18, 29-44.
- Quinn, TP. 2004. *The behavior and ecology of Pacific salmon and trout*. Univ. Press, ISBN: 0-295-98457-0, Seattle, USA.
- Raymond M. & Rousset F. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity*, 86, 248-249.
- Rivinoja, P. 2005. *Migration problems of Atlantic salmon (Salmo salar L.) in flow regulated rivers*. Doctoral thesis, Swedish University of Agricultural Sciences, Umeå. ISSN 1652-6880, ISBN 91-576-6913-9. Umeå, Sweden.
- Ruzzante, D.E., Hansen, M.M. & Meldrup, D. 2001. Distribution of individual inbreeding coefficients, relatedness and influence of stocking on native anadromous brown trout (*Salmo trutta*) population structure. *Molecular Ecology* 10, 2107-2128.
- Ruzzante, D.E., Hansen, M.M., Meldrup, D. & Ebert, K.M. 2004. Stocking impact and migration pattern in an anadromous brown trout (*Salmo trutta*) complex: where have all the stocked spawning sea trout gone? *Molecular Ecology* 13(6), 1433-1445.
- Ryder, O.A. 1986. Species conservation and systematics: the dilemma of subspecies. *Trends in Ecology and Evolution* 1, 9-10.
- Ryman, N. & Laikre, L. 1991. Effects of Supportive Breeding on the Genetically Effective Population Size. *Conservation Biology* 5, 325-329.
- Ryman, N. & Ståhl, G. 1981. Genetic perspectives on the identification and conservation of Scandinavian stocks of fish. *Canadian Journal of Fisheries and Aquatic Sciences* 38, 1562-1575.

- Ryman, N. 1983. Patterns of distribution of biochemical genetic variation in salmonids: differences between species. *Aquaculture* 33, 1-21.
- Ryman, N., Allendorf, F.W. & Ståhl, G. 1979. Reproductive isolation with little genetic divergence in sympatric populations of brown trout (*Salmo trutta*). *Genetics* 92: 247-262
- Schneider, S., Kueffer, J.-M., Roessli, D. & Excoffier, L. 1997. Arlequin, Version 1.1, Genetics and Biometry Laboratory, Department of Anthropology, University of Geneva, Geneva, Switzerland.
- Schön, L. 2000. *En modern svensk ekonomisk historia. Tillväxt och omvandling under två sekel.* (In Swedish) SNS förlag, Stockholm, Sweden.
- Scruton, D.A., Anderson, T.C. & King L.W. 1998. Pamehac Brook: A case study of the restoration of a Newfoundland, Canada, river impacted by flow diversion for pulpwood transportation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 8, 145-157.
- Scruton, D.A., Pennell, C.J., Bourgeois, C.E., Goosney, R.F., Porter, T.R. & Clarke, K.D. 2006. Assessment of a retrofitted downstream fish bypass system for wild Atlantic salmon (*Salmo salar*) smolts and kelts at a hydroelectric facility on the Exploits River, Newfoundland, Canada. *Hydrobiologia* (In press).
- Spedicato, M.T., Lembo, G. & Marmulla. (eds) 2005. *Aquatic telemetry: advances and applications. Proceedings of the fifth conference of fish telemetry held in Euorpe, Ustica, Italy, 9-13 June, 2003.* ISBN: 92-5-105301-4 Rome, FAO/COISPA. 295p.
- Stabell, O.B. 1984. Homing and olfaction in salmonids: A critical review with special reference to the Atlantic salmon. *Biological Reviews of the Cambridge Philosophical Society*. 59, 333-388.
- Stridsman, S. 1995. Fiskevårdsåtgärder i Hartijoki, Kalixälvens vattensystem 1992-1994. Fiskeriverket, Utredningskontoret i Luleå. (In Swedish), Luleå.
- Stuart, T.A. 1957. The Migrations and Homing Behaviour of Brown Trout (*Salmo trutta* L.). *Freshwater and Salmon Fisheries Research* 18, 1-27.
- Svendsen, J.C., Koed, A. & Aarestrup, K. 2004. Factors influencing the spawning migration of female anadromous brown trout. *Journal of Fish Biology* 64, 528-540.
- Säisä, M., Koljonen, M.-L., Gross, R., Nilsson, J., Tähtinen, J., Koskiniemi, J. & Vasemägi, A. 2005. Population genetic structure and postglacial colonization of Atlantic salmon (*salmo salar*) in the Baltic Sea based on microsatellite DNA variation. *Canadian Journal of Fisheries and Aquatic Sciences* 62, 1887-1904.
- Thorstad, E.B. 2006. Factors affecting the within spawning migration of Atlantic salmon, with emphasis on human impacts. PhD-dissertation Thesis 2006. Norwegian Institute for Nature Research.
- Thorstad, E.B., Okland, F. & Finstad, B. 2000. Effects of telemetry transmitters on swimming performance of adult Atlantic salmon. *Journal of Fish Biology*. 57, 531-535.
- Trepanier, S., Rodriguez, M.A. & Magnan, P. 1996. Spawning migrations in landlocked Atlantic salmon: Time series modelling of river discharge and water temperature effects. *Journal of Fish Biology* 48, 925-936.
- Törnlund, E. 2002. "flottningen dör aldrig" Bäckflottningens avveckling efter Ume- och Vindelälven 1945 - 70. Umeå Studies in Economic History, Umeå ISSN 0347-254-X ISBN 91-7305-374-0, Umeå, Sweden.
- Utter, F.M. 1991. Biochemical genetics and fisheries management: an historical perspective. *Journal of Fish Biology* 39, 1-20.
- Wang, J. & Ryman, N. 2001. Genetic Effects of Multiple Generations of Supportive Breeding. *Conservation Biology* 15, 1619-1631.
- Waples, R.s. & Gaggiotti, O. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology* 15, 1419-1439.
- Waples, R.S. 1995. Evolutionary significant units and the conservation of biological diversity under the endangered species act. *American Fisheries Society Symposium* 17, 8-27.
- Ward, R.D. 2000. Genetics in fisheries management. *Hydrobiologia* 420, 191- 201.
- Vasemägi, A. 2004. *Evolutionary Genetics of Atlantic Salmon (Salmo salar L.)* Doctoral thesis. Department of Aquaculture, Swedish University of Agricultural Science, Umeå. ISSN 1401-6230 ISBN 91-576-6708-X, Umeå, Sweden.

- Webb, J. 1989. The movements of adult Atlantic salmon in the River Tay. *Scottish Fisheries Research Report* 44, 1-32.
- Winter, J. 1996. Advances in Underwater Biotelemetry. p. 555-590 *In Fisheries Techniques*, 2nd Ed, Murphy BR, Willis DW (eds). American Fisheries Society, Bethesda Maryland, USA.
- Økland, F., Erkinaro, J., Moen, K., Niemelä, E., Fiske, P., McKinley, R.S. & Thorstad, E.B. 2001. Return migration of Atlantic salmon in the River Tana: phases of migratory behaviour. *Journal of Fish Biology* 59, 862-874.
- Östlund, L., Zackrisson, O. & Axelsson, A.-L. 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forestry Research* 27, 1198-206.
- Östergren, J. 2003. Öringracet: Radiomärkning för att följa havsöringens lekvandring i Vindelälven och Piteälven. Rapport 1, 2002. Arbetsrapport. Institutionen för vattenbruk, SLU, Umeå.